

ELASMOSAUR (REPTILIA: PLESIOSAURIA) BASICRANIAL REMAINS FROM THE EARLY CRETACEOUS OF QUEENSLAND

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A near complete basioccipital and associated elements belonging to a juvenile elasmosaur are described from the Early Cretaceous (upper Albian) of northern Queensland. This is the first record of well-preserved elasmosaur basicranial remains from Australia. The basioccipital is comparable to those known from other elasmosaurs but is unusual in the contribution of the exoccipital-opisthotic facet to the margin of the occipital condyle (but not to its articular surface) and dorsal termination of the condylar groove. The significance of this morphology is discussed.

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Examination of juvenile elasmosaur remains (AM F87826) from the Early Cretaceous of Queensland has revealed a previously unrecognised near complete basioccipital. This represents the first record of well-preserved elasmosaur basicranial remains from Australia. The cranial remains of Australian elasmosaurs are extremely rare, being confined to a single badly crushed skull (QM F11050) in which the basicranium is obscured by overlying elements and matrix. This specimen was tentatively attributed to the genus *Woolungasaurus* by Persson (1982); however, Thulborn & Turner (1993) reassigned it to Elasmosauridae indet., following Welles (1962) who considered *Woolungasaurus* a *nomen dubium*. A small tooth-bearing bone interpreted as a plesiosauroid maxilla by Longman (1935) was shown to be an ichthyosaurian premaxillary, maxillary or dentary fragment by Persson (1960). This paper describes the recovered basioccipital and associated elements of AM F87826, and provides a brief character analysis of plesiosaur basioccipital morphology.

Cranial terminology follows Andrews (1910, 1913), Brown (1981) and Cruickshank (1994). Institutional abbreviations: AM, Australian Museum, Sydney; QM, Queensland Museum, Brisbane; UWA, University of Western Australia, Perth. All measurements were taken using callipers and are in millimetres (mm).

SYSTEMATICS

Class REPTILIA

Subclass SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Superfamily PLESIOSAUROIDEA (Gray, 1825) Welles, 1943

Family ELASMOSAURIDAE Cope, 1869

Elasmosauridae genus and species indet.

Material

AM F87826, a partial neck and base of skull including the basioccipital, at least 33 cervical centra, parts of the neural arches, several partial cervical ribs and miscellaneous fragments. Lack of fusion between basicranial elements and associated vertebral centra, neural arches and cervical ribs indicates that the specimen is a juvenile.

Locality

'Dunraven' Station, near Hughenden, central-northern Queensland. Toolebuc Formation, upper Albian (Day 1969; Smart & Senior 1980).

Diagnosis

Basioccipital condyle with a squared dorsal margin and heart-shaped condylar outline. Exoccipital-opisthotic facets of the basioccipital contribute to the occipital condyle margin but do not form part of the condylar surface. Groove circumscribing the basioccipital condyle terminates dorsally at the posterolateral edges of the exoccipital-opisthotic facets. Cervical centra platycoelous with articular surfaces having an open V-shaped cross-section and margins which form an abrupt angle with the centrum sides. Length of the anterior cervical centra is greater than their height. Lateral surfaces of cervical centra bear distinct longitudinal ridges.

Description

Basioccipital. (Fig. 1, Table 1).

The basioccipital has suffered damage to the left pterygoid facet but is otherwise well preserved. The anterior basioccipital surface is dominated by a prominent, deeply rugose facet

TABLE 1. Measurements (mm) of basioccipital AM F87826, * - not including missing pterygoid facet portion

| Description | mm |
|--|------|
| Total length | 29.3 |
| Total width* | 34.9 |
| Width across exoccipital-opisthotic facets | 24.4 |
| Condyle diameter | 19.8 |

for contact with the basisphenoid. This is dorsoventrally compressed and reniform in outline, extending partly onto the anteroventral surface of the basioccipital. The dorsal-most facet margin is produced into a narrow transverse ridge, which borders the posteriorly inclined anterodorsal surface. This bears a prominent circular depression with median pit probably representing part of the posterior wall of the pituitary fossa or dorsum sellae (Cruickshank 1994). Chatterjee & Small (1989)

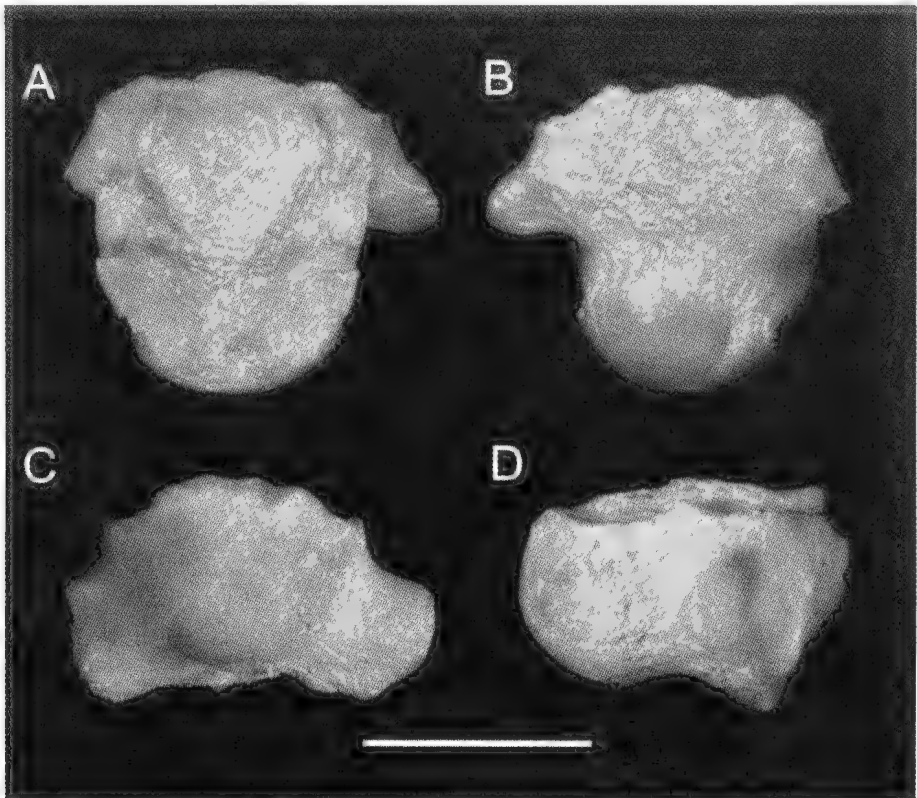


FIGURE 1. Basioccipital of AM F87826 in (A) dorsal, (B) ventral, (C) posterior and (D) lateral views. Scale bar is 20 mm.

interpreted a similar pit in the basioccipital of *Morturneria* (from the Maastrichtian of Antarctica) as representing the 'hypophyseal-basiscrania' fenestra. The anterodorsal circular depression is medially subdivided by a shallow vertical groove and bordered laterally by deep longitudinal channels. These extend posteriorly onto the rugose dorsal surface. The dorsal surface of the basioccipital bears a pair of broad ovoid facets for the exoccipital-opisthotic elements, which form part of the condylar margin but do not contribute to the articular surface (comprised entirely of the basioccipital). Between the exoccipital-opisthotic facets is the spindle-shaped floor of the endocranial cavity. Anteriorly, this expands into a raised triangular plateau, which bears a shallow longitudinal depression (extending to a notch in the anterodorsal margin of the dorsum sellae) possibly representing the sella turcica (see Welles & Bump 1949). Anteriorly, the exoccipital-opisthotic facets are separated from the small circular prootic facets by low transverse ridges. The anterior prootic facet margin is raised and irregular suggesting the presence of cartilage, possibly supporting a forward expansion of the prootic onto the basisphenoid. The anterolateral basioccipital surfaces are produced into short, massive pterygoid processes, which terminate in anterolaterally oriented, triangular pterygoid facets. The pterygoid facet surfaces are smooth and separated anteromedially from the rugose basisphenoid facet by a prominent vertical flange. The basioccipital condyle is rounded, lacks a notochordal pit and is weakly heart-shaped in outline, with the squared dorsal margin forming the edge of the foramen magnum. The condylar surface is partly circumscribed by a shallow groove which terminates dorsally at the posterolateral edges of the exoccipital-opisthotic facets.

Axial skeleton. (Fig. 2, Table 2).

At least 33 complete to fragmentary cervical vertebrae have been recovered, representing portions of the anterior (Figs 2A, 2B), middle (Figs 2C, 2D) and posterior (Figs 2E, 2F) cervical series. Fragmentary remains of the neural arches and some cervical ribs are also preserved. The anterior cervical centra are cylindrical and somewhat dorsoventrally compressed with centrum length always exceeding the height. This trend is lost in the middle and posterior cervical series where the centrum width exceeds the

length. There is a marked increase in overall size of the cervical centra from the anterior to posterior section of the neck.

The articular surfaces of the centra are platycoelous, smooth and ovoid in outline, becoming near elliptical posteriorly. In transverse cross-section, the articular surfaces of all centra are an open V-shape, with the margins of the face forming an abrupt angle with the centrum sides. A small notochordal pit shallowly indents the centre of each articular surface. Dorsally, each centrum bears a prominent median hourglass-shaped

TABLE 2. Measurements (mm) of AM F87826 vertebral centra. Numbering of centra begins at the anterior-most and does not include the atlas or axis. A gap including an unknown number of centra is present between C27 and C28. * - centrum represented only by fragments

| Element | Length | Width | Height |
|---------|--------|-------|--------|
| C1 | 24.9 | 22.2 | 17.7 |
| C2 | 26.4 | 22.9 | 19.1 |
| C3* | - | - | - |
| C4 | - | - | 21.5 |
| C5 | - | - | 28.1 |
| C6 | 39.4 | - | 26.4 |
| C7 | 42.9 | - | 29.4 |
| C8 | - | 33.5 | 22.2 |
| C9* | - | - | 31.1 |
| C10 | 49.8 | - | 33.9 |
| C11 | 61.3 | - | - |
| C12* | - | - | - |
| C13 | - | - | 52.4 |
| C14 | 63.6 | - | - |
| C15 | 62.7 | 70.8 | 49.8 |
| C16 | 67.4 | - | 50 |
| C17 | 65.1 | 74.7 | 53.9 |
| C18 | 64.8 | 73.9 | 53.1 |
| C19 | - | 75.6 | - |
| C20 | 65.2 | 74.5 | 54.3 |
| C21 | 67.1 | - | 55.9 |
| C22 | 66.8 | 78.7 | 56.4 |
| C23 | 67.8 | 78.5 | 56 |
| C24 | 66.7 | 80.1 | - |
| C25 | 67.7 | 78.3 | 56.8 |
| C26 | 66.7 | 79.3 | - |
| C27 | 61.6 | 91.3 | 58.9 |
| C28* | - | - | - |
| C29* | - | - | - |
| C30 | 54.2 | 85.2 | 50.2 |
| C31 | - | 80.6 | - |
| C32 | 44.2 | 90.6 | 60.4 |
| C33 | 57.4 | 93.1 | 61.2 |

depression marking the neural canal. In the anterior-most vertebra, this becomes transversely narrow towards the anterior margin of the centrum where the depression is bordered laterally by the large ovoid facets for the neural arches. The neural arch facets are deeply concave and situated close to the anterior margin, becoming more centrally placed and extending to the edges of both the anterior and posterior articular facet rims in successive centra. The neural arch facets are separated ventrally from the elliptical cervical rib facets by the deeply concave lateral centrum surface. The lateral surface of each centrum bears a distinct longitudinal ridge. The rib facets are

raised, deeply concave and situated close to the posterior articular rim. The ventral surface of each anterior centrum is markedly concave and bears paired nutrient foramina separated by a broad median-ventral keel. The nutrient foramina become progressively more laterally placed in successive vertebra with a corresponding reduction in prominence of the mid-ventral keel.

The neural arches are fragmentary but preserve parts of the neural arch body and neural spines. The neural arches possess thin lateral walls enclosing the neural canal, and deeply excavated anterior surfaces. The anterior excavation is tall and elliptical in outline with a narrow median

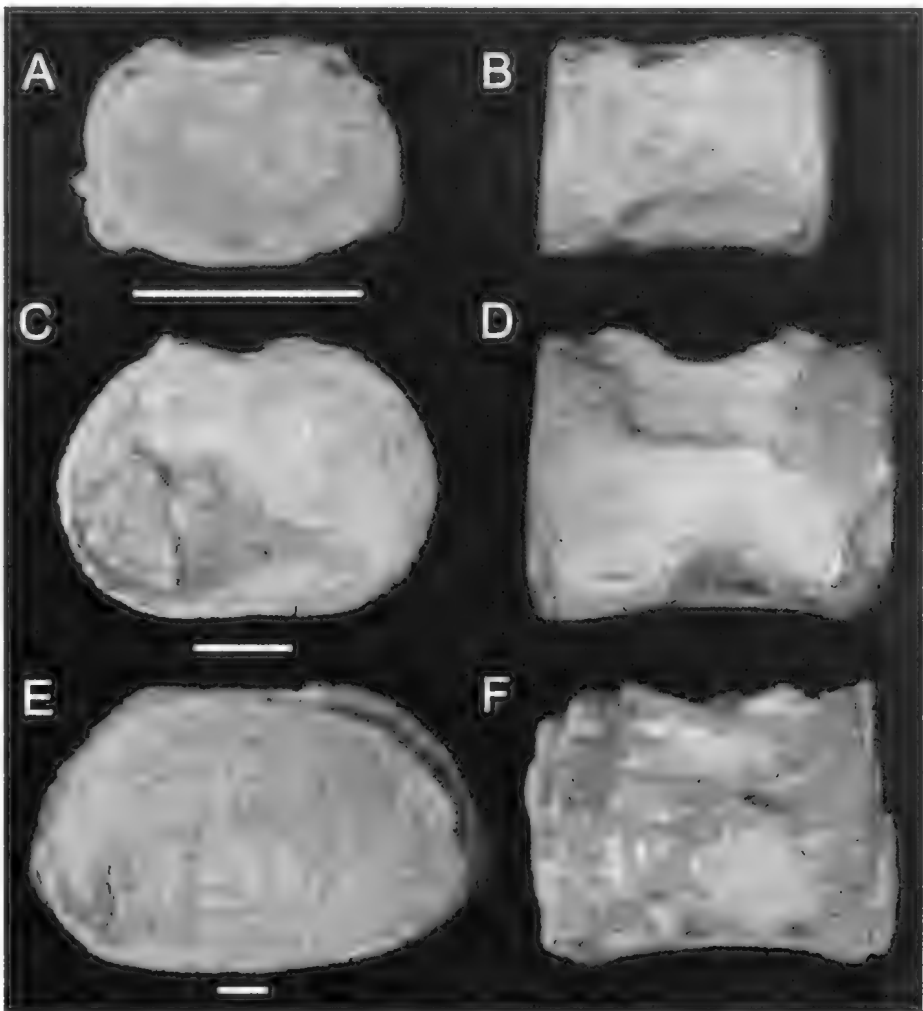


FIGURE 2. AM F87826 anterior (C2) cervical centrum in (A) anterior and (B) lateral views; middle (C15) cervical centrum in (C) anterior and (D) lateral views; and posterior (C27) cervical centrum in (E) anterior and (F) lateral views. Scale bars are 20 mm.

vertical septum. The neural spine fragments are strongly transversely compressed and elliptical in cross-section.

All recovered cervical ribs are fragmentary and lack unequivocal associations with the centra. The cervical ribs are all single headed with anteroposteriorly elongate and ovoid articular facets. The articular facet surface is concave and finely pitted with slightly flared flange-like margins. The rib shafts are dorsoventrally compressed and elliptical in cross-section.

Remarks

AM F87826 is comparable in its vertebral morphology to Cretaceous elasmosaurid material from elsewhere in Australia (eg Persson 1960, 1982; Murray 1987), particularly isolated remains from unspecified (probably Albian) deposits near Oodnadatta (Freytag 1964), and the Neales River region (SAM P6181, Persson 1960), South Australia; and the Late Cretaceous (Cenomanian–Turonian) Molecap Greensand, Western Australia (UWA 22034, Long & Cruickshank 1998). All of these specimens exhibit proportionately short posterior cervical centra.

AM F87826 can be assigned to *Elasmosauridae* indet. on the basis of: (1) platycoelous articular surfaces on the cervical centra. The presence of platycoelous articular surfaces is considered an elasmosaurid synapomorphy by Brown (1981, 1993) and Bardet et al. (1999). The character-state is also known to occur in the Maastrichtian cryptoclidid *Morturneria* (Chatterjee & Small 1989), however this taxon has more recently been reinterpreted as a derived elasmosaurid (Bardet et al. 1991); (2) articular surfaces of cervical centra with open V-shaped cross-section and margins which form an abrupt angle with the centrum sides. This is an apomorphic state potentially uniting all members of the *Elasmosauridae* (Brown 1993; Bardet et al. 1999) and can be distinguished from the plesiomorphic condition in cryptoclidids and plesiosaurids, in which the articular surfaces are sigmoidal in cross-section with a raised convex rim (Brown et al. 1986; Brown 1993); (3) anterior cervical centra with length greater than their height. The presence of anterior cervical centra which are elongate relative to their height is an unequivocal synapomorphy of all elasmosaurids (Welles 1952; Brown 1993; Bardet et al. 1999); (4) lateral longitudinal ridges on the cervical centra. Prominent longitudinal ridges are present on the lateral surfaces of the cervical centra in all elasmosaurids, representing a potential synapomorphy for the group (Welles 1943, 1952, 1962; Brown 1993; Bardet et

al. 1999). Brown (1981), however, noted that the feature is variable with ontogeny, being less well developed in younger individuals.

COMPARISONS AND DISCUSSION

AM F87826 is comparable in its basioccipital morphology to other elasmosaurs, particularly *Libonectes* which also exhibits a squared dorsal condylar margin and heart-shaped condylar outline (Carpenter 1997). The specimen is unusual, however, in the exoccipital-opisthotic facets participating in the condylar margin, and subsequent dorsal termination of the condylar groove. This differs from the common condition in elasmosaurs, and most other plesiosaurids, in which the condylar groove completely circumscribes the occipital condyle, excluding it from contact with the exoccipital-opisthotic facets (Welles 1962; Brown 1981; Bardet et al. 1999). Exclusion of the exoccipital-opisthotic facets from the condylar rim is also known to occur in nothosaurids (Rieppel 1994). A character-state similar to that of AM F87826 is present in the Rhaetian/Hettangian taxon *Thalassiodracon* (Storrs & Taylor 1996) and the Maastrichtian *Morturneria* (Chatterjee & Small 1989). Such comparable morphology may be the result of convergence in the case of *Thalassiodracon* (as suggested by the presence of the plesiomorphic condition in nothosaurids and most plesiosaurids including elasmosaurids); however, the recent reclassification of *Morturneria* as a derived elasmosaurid (Bardet et al. 1991) does raise the possibility of homology. Distinct condyle–facet contact is also known to occur in *Cryptoclidus* (Andrews 1910; Brown 1981), *Kimmerosaurus* (Brown 1981), *Eurycleidus* (Cruickshank 1994) and pliosaurids (Andrews 1913) but involves contribution of the exoccipital-opisthotic to the basioccipital articular surface and absence of a distinct condylar groove. AM F87826 can therefore be interpreted as autapomorphic in its condylar morphology.

Incomplete dorsal closure of the condylar groove may, alternatively, represent an ontogenetic feature similar to the variable groove development present in juvenile specimens of *Muraenosaurus* (Brown 1981). Complete separation of the exoccipital-opisthotic facets and occipital condyle in all growth stages of *Muraenosaurus* (Brown 1981), however, supports interpretation of the facet–condyle contact in AM F87826 as a potentially apomorphic character state.

Molnar (1991) suggested that Australian plesiosaur faunas lacked extensive regional endemism and were composed of largely cosmopolitan forms. While this is almost certainly true for higher taxonomic categories, the presence of potentially autapomorphic elasmosaur remains suggests that at least some distinct taxa may have inhabited the Australian epicontinental seaway and surrounding coastal regions of eastern Gondwana during the Early Cretaceous.

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